

Egg masses of three gastropods, *Kerguelenella lateralis* (Siphonariidae), *Laevillatorina caliginosa* and *Macquariella hamiltoni* (Littorinidae), from Macquarie Island (sub-Antarctic).

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ABSTRACT

The egg masses of three species of sub-Antarctic gastropods (*Kerguelenella lateralis*, *Laevillatorina caliginosa* and *Macquariella hamiltoni*) are described. Each species has non-pelagic development in the egg-masses and the relationships of this reproductive strategy to geographical position and egg size are discussed.

INTRODUCTION

The modes of larval development and the reproductive cycles of a number of molluscs and echinoderms from the sub-Antarctic Macquarie Island (54°38'S 158° 53'E) have been previously described (Simpson, 1977, 1982). The egg masses of two gastropod species, *Kerguelenella lateralis* and *Macquariella hamiltoni*, were found during those studies. For a third species, *Laevillatorina caliginosa*, a prediction of non-pelagic development via the laying of an egg mass was made from the number and size of ova in the ovaries of preserved specimens (Simpson, 1977). A subsequent visit to Macquarie Island confirmed the prediction. The egg masses of these three species are described here.

Marine benthic invertebrates in high latitudes have a tendency towards a non-pelagic mode of larval development (Thorson, 1950; Mileikovsky, 1971; Simpson, 1977; Jablonski and Lutz, 1983). The most favoured hypothesis to explain this trend is that slow development rates of larvae in cold water, together with the limited period of seasonal production of phytoplankton food, make it difficult for planktotrophic larvae to complete their development. (However, Clarke (1982) has suggested that slow development rates of invertebrates in polar latitudes have evolved to allow release of advanced, competitive young — as an adaptation to the pattern of food supply to the benthic marine environment. That is, slow development is not the direct result of low temperature.)

Non-pelagic modes of larval development in high latitudes have also been related to: harsh conditions in surface waters for larvae, increased predation for slower developing larvae, availability of suitable substrate for larval settlement, the connection between greater variability in survival of early growth stages and the K- model for reproductive strategy, and decrease in adult size. Further data on the modes of larval development of marine invertebrates across all latitudes will assist the interpretation of the above trend. As Picken (1979) noted, the majority of records are from the northern hemisphere. The southern hemisphere presents a different suite of physical, climatic, and biogeographical factors for any biological phenomenon acting across a latitudinal gradient. Consequently, additional data from the southern hemisphere are especially valuable to elucidate any shift in emphases resulting from components of these factors.

Apart from contributing to the specific objective of obtaining further information to aid in the interpretation of Thorson's Rule, the descriptions of the egg masses of these three species simply add to the knowledge of the life history of the animals. Such information can then be used in future comparisons, whatever the reason, within and across taxa.

METHODS AND COLLECTION SITES

Over a one year period, monthly collections of a number of molluscs and echinoderms were made from the littoral and sublittoral zones of Macquarie Island for the purposes of determining reproductive cycles (Simpson, 1977, 1982). During this time, egg masses of the siphonariid limpet, *Kerguelenella lateralis*, and the littorinid, *Macquariella hamiltoni*, were collected towards the end of the one year collecting period (in the late spring/summer of 1968-69). During subsequent visits to Macquarie Island (in the late spring/summer of 1979/80 and late spring of 1981), further collections of egg masses of these two species were made. Also, during the two latter trips, egg masses of the littorinid, *Laevilitorina caliginosa*, were found and collected. All collections were preserved in Baker's formol-cobalt-calcium (Simpson, 1977).

Egg masses were not observed being laid. However, the following indirect evidence provides sufficient assurance that egg masses have been correctly assigned to each species. For *K. lateralis*: this is the only siphonariid on Macquarie's shores. Further, egg masses were collected from rock surfaces inhabited by no other gastropod species. For *M. hamiltoni*: as mentioned in Simpson (1977), egg masses were taken from red algae on which only adult *M. hamiltoni* were present. Also, the confined spaces of many of the sites of the deposited egg masses (at the bases of multi-branched stipes) infer that the layer was a small mollusc. For *L. caliginosa*: the egg masses were collected from rock surfaces on which adult *L. caliginosa* were abundant. The only other gastropod molluscs in the vicinity were *K. lateralis* and the limpet *Nacella (Patinigera) macquariensis*. A third littorinid species is known from Macquarie Island — *Macquariella macphersonae* (Dell, 1964). Adult littorinids were collected at the same time as the egg masses from both the algae and the rock surfaces. No specimens of *M. macphersonae* were found in those collections of adults.

K. lateralis is the dominant organism of one of the prominent zones on the rocky shores of Macquarie Island — the "Bare" Zone, located in the middle region of the eulittoral zone (Kenny and Haysom, 1962; Simpson, 1976). (The term "Bare" designates a zone lacking in macroscopic algae, which dominate the remaining parts of the shore.) Within this zone, egg masses of *K. lateralis* were found, often deposited in shallow crevices and channels. *L. caliginosa* extended high into the eulittoral zone where it is usually found in pools or on the under-surfaces of rocks. Egg masses of *L. caliginosa* were taken from rock surfaces in these habitats. Egg masses of *Macquariella hamiltoni* were found on red algae, particularly *Rhodymenia* sp., at the bottom of the eulittoral zone. The egg masses were predominantly located towards the bases of the algal fronds. The vertical range of *Macquariella hamiltoni* is from the upper sublittoral to the lower eulittoral regions where they are most commonly found attached to red algae.

RESULTS

Table 1 lists the data for the sizes of the egg masses and the eggs, and for the number of eggs per egg mass, of all three species. The data are taken only from egg masses that were collected whole and undamaged.

Figure 1 shows lateral and dorsal views of an egg mass of *K. lateralis* and a late stage embryo, prior to hatching. Figure 2 shows dorsal views of egg masses of *L. caliginosa* with embryos at early and late stages while Fig. 3 shows the same for *M. hamiltoni*. The egg masses of *M. hamiltoni* were deposited in a single layer while those of *L. caliginosa* were laid in a round hump with some eggs overlying others.

For *K. lateralis*, egg masses often had a number of compartments with no eggs in them (see Fig. 1) and these were not included in the above calculations. The number of empty compartments per mass ranged from 0 to 11, with only one egg mass having no empty compartments. There were also empty compartments in the egg masses of *L. caliginosa* and *M. hamiltoni* but far fewer than were found for *K. lateralis*; that is, there were empty compartments in 60% of the masses of *L. caliginosa* (ranging from 1 to 6) and in 35% of the masses of *M. hamiltoni* (ranging from 1 to 5). Again, these empty compartments were not used in the calculations of number of eggs per mass.

The number of eggs per mass showed considerable variation in *K. lateralis* and *M. hamiltoni* but a component of this variation was due to low scores of number of eggs in masses having high numbers of empty compartments.

L. caliginosa lays a larger egg mass than *M. hamiltoni* with a higher number of eggs per mass; the sizes of the eggs in the two species are similar.

DISCUSSION

Typically, members of the Family Siphonariidae lay a benthic egg mass from which planktonic veligers hatch (Berry, 1977). Pelagic egg masses have been described for two south-east Australian species of *Siphonaria*: *S. virgulata* (Creese, 1980) and *S. tasmanica* (Quinn, 1983). (*S. virgulata* has since been designated as a geographical variant of, and hence synonymous with, *S. funiculata* (Jenkins, 1981)). From these pelagic egg masses, the larvae hatch as planktonic veligers. A non-pelagic development to a juvenile stage within the egg mass has been recorded previously in two species: the tropical *Siphonaria kurracheensis* (Thorson, 1940) and the sub-Antarctic *Kerguelenella stewartiana* (Knox, 1955).

The egg masses of *K. lateralis* are very similar to those described for *K. stewartiana* by Knox (1955) — that is, a tough, gelatinous, transparent mass containing a number of compartments (cocoons). The egg masses and a fully developed embryo of *K. stewartiana*, as illustrated by Knox (1955), are shown in Fig. 4 for comparison. The eggs of *K. lateralis* appear to be slightly smaller than those of *K. stewartiana* ($1.26 \text{ mm} \pm 0.27 \text{ S.D.}$ in *K. lateralis* vs. a range of 1.35 — 2.00 mm in *K. stewartiana*). However, the egg measurements of *K. lateralis* did not include the housing compartment which was apparently included in the measurements for *K. stewartiana* by Knox (1955). This would increase the dimension by approximately 0.2 mm. Also, *K. lateralis* had a greater number of eggs per mass ($24.3 \pm 10.2 \text{ S.D.}$ vs. 9 to 35) (Knox (1955)) gave two ranges for eggs per egg mass: 9 to 35 and 12 to 25); however, this may simply be related to the smaller sizes of *K. stewartiana* (maximum length 15.5 mm), compared to those of *K. lateralis* (maximum length 20.8 mm) from the two study areas. From these records, *K. stewartiana* appears to be a slightly smaller species than *K. lateralis*. The similarities in the reproductive modes of the two species are very striking: the reproductive strategy itself, the structure of the egg mass, and the external appearance of the embryo prior to hatching. These similarities indicate that a closer examination of *K. lateralis* and *K. stewartiana* would be worthwhile to verify whether they are two separate species.

These two species of *Kerguelenella* conform to "Thorson's Rule" — the tendency towards a non-pelagic mode of larval development for those members of a taxonomic group that inhabit high latitudes. *S. kurracheensis*, being a tropical siphonariid with non-pelagic development, goes against the trend. However, these three siphonariid species live in, or extend into, the high littoral and it is tempting to suggest that non-pelagic development may have some adaptive advantage for siphonariids occupying this part of the shore. However, such simple correlations are invariably offset with contrary examples, as has been found in other groups — e.g. Littorinidae (Mileikovsky, 1975).

From comparisons with data for other Siphonariidae there is a predictability between egg size and mode of larval development; that is, large eggs (>0.35 mm) indicate non-pelagic development while below that size indicates pelagic development (Table 2). Also, with smaller eggs there are many more eggs per mass. Differences in the size of the egg mass and the corresponding number of eggs per mass for any species would be largely due to different sizes of the spawning parent, as was shown for *Siphonaria denticulata* by Creese (1980).

As previously reported (Simpson, 1977), the egg masses of *K. lateralis* were often invaded by oligochaete worms, particularly in the upper parts of the siphonariid's range. However, the empty compartments of *K. lateralis*, and of the two littorinid species, reported here had no macroscopic organisms within the egg masses. The empty compartments could have resulted from more subtle invasion or predation by micro-organisms, or from the molluscs' failure to deposit an egg into an egg compartment.

Many species of Littorinidae inhabit the highest regions of the littoral zone where there are likely to be special adaptations for reproduction in the harsh, aerial conditions. In a review of larval development in the Littorinidae, Mileikovsky (1975) found that associations could be drawn for ovoviviparity in the littoral fringe (called "supralittoral" by Mileikovsky) and for non-pelagic development via benthic egg masses in the eulittoral zone (called "littoral" by Mileikovsky); however, pelagic larval development occurred in littorinid species from all parts of the shore. Mileikovsky rejected the previously held concept of obligate interrelationships between definite types of larval development in marine benthic invertebrates and their existence in definite ecological zones on the shore. The two species of littorinids in this study occupy wet habitats. *L. caliginosa* extends up to the top of the eulittoral zone but its habitats are pools or the undersurfaces of boulders. The findings provide two further instances of non-pelagic development in a group that exhibits a variety of reproductive strategies.

Both *L. caliginosa* and *M. hamiltoni* are small molluscs, *L. caliginosa* being the slightly larger of the two (5.0 mm maximum length vs 4.0 mm for *M. hamiltoni*). The larger egg mass and the greater number of eggs per mass for *L. caliginosa* may be due simply to its larger size. However, this does not necessarily mean that *L. caliginosa* has a greater fecundity. *M. hamiltoni* may lay more egg masses per individual than *L. caliginosa*.

Comparisons with data for other Littorinidae show a relationship between egg size and pelagic vs non-pelagic development as is the case in the Siphonariidae: large eggs indicate a totally non-pelagic development and small eggs indicate pelagic development (Table 3). Such a relationship apparently results from the greater amount of yolk required for the embryo to reach a crawling, juvenile stage.

For all three species, egg masses were collected throughout the spring-summer period. During that time, egg masses were found with stages ranging from undifferentiated eggs to shelled embryos. Whether egg masses were laid at other times of the year for the littorinids is not known. Egg masses of *K. lateralis* were observed at other times of the year but no collections were made then. The presence of mature ova and spermatozoa in the three species throughout the year (Simpson, 1977) suggests that egg-laying is continuous although it may be held over during some parts of the year.

A likely consequence of non-pelagic development is restricted dispersal resulting in a narrow geographical range. However, *K. lateralis* and *L. caliginosa* have a wide circum — Southern Ocean distribution and *M. hamiltoni* has been found at Heard Island (Dell, 1964). For *K. lateralis* and *L. caliginosa*, the egg masses are firmly cemented to the rocky substrate and the chances of these

egg masses being washed into the sea are extremely remote. Egg masses of *M. hamiltoni* could become sea-borne on dislodged algae. Adults of many species may be rafted around the Southern Ocean on dislodged, floating kelps. Arnaud (1974) listed many invertebrate inhabitants of the kelps of the Kerguelen Islands and proposed that the kelps acted as a dispersal agent for many sub-Antarctic marine invertebrates. *L. caliginosa* and *M. hamiltoni* have been recorded as commonly occurring in the holdfasts of *Durvillea antarctica* (Kenny and Haysom, 1962; Simpson, personal observations) and *L. caliginosa* has been recorded on *Macrocystis* sp. at South Georgia (Arnaud and Bandel, 1978). The wide geographic range of *K. lateralis* is somewhat puzzling as this species has not been recorded as occurring on such kelps.

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TABLE 1. Egg masses (dimensions and numbers of eggs) and egg sizes — for *K. lateralis*, *L. caliginosa* and *M. hamiltoni*.

Egg mass dimensions:		Eggs:	
<i>K. lateralis</i>	33	<i>K. lateralis</i>	21
<i>L. caliginosa</i>	30	<i>L. caliginosa</i>	20
<i>M. hamiltoni</i>	17	<i>M. hamiltoni</i>	16
n		n	
Mean length, mm (\pm S.D.)	5.4 (\pm 1.1)	Range	13-55
	2.2 (\pm 0.5)	Mean (\pm S.D.)	24.3 (\pm 10.2)
	1.9 (\pm 0.4)		12.2 (\pm 2.5)
			6.0 (\pm 2.2)
		No. of eggs per mass	2-9
			13-55
			9-19
			12.2 (\pm 2.5)
			6.0 (\pm 2.2)
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TABLE 2. Number of eggs per mass, egg sizes, and ecological mode of embryonic development in some Siphonariidae.

Species	No. of eggs per mass	Egg diameter (μm)	Mode of development	Source
<i>Kerguelenella stewartiana</i>	9-35	1,350 - 2,000	Non-pelagic	Knox, 1955
<i>Kerguelenella lateralis</i>	13-55	1,260 \pm 270 SD	Non-pelagic	This paper
<i>Siphonaria kurracheensis</i>	Hundreds	380 - 500	Non-pelagic	Thorson, 1940
<i>Siphonaria virgulata</i> (= <i>S. funiculata</i>)	9,200	100	Pelagic	Creese, 1980
<i>Siphonaria denticulata</i>	12,200-26,800	100	Pelagic	Creese, 1980
<i>Siphonaria tasmanica</i>	Thousands*	94.9 \pm 6.1 SD	Pelagic	Quinn, 1983
<i>Siphonaria japonica</i>	Thousands*	87 - 91	Pelagic	Abe, 1940

*Inferred from illustration.

TABLE 3. Egg sizes and ecological mode of embryonic development in some Littorinidae.

Species□	Egg diameter* (μm)	Mode of development	Source
Pelagic development:			
<i>Nodilittorina pintoado</i>	60 - 70	Spawned as eggs	Struhsaker, 1966
<i>Nodilittorina picta</i>	70 - 80	Spawned as eggs	Struhsaker, 1966
<i>Nodilittorina acutispira</i>	75 - 93	Spawned as eggs	Underwood and McFadyen, 1983
<i>Littorina zigzac</i>	80	Spawned as eggs	Lebour, 1945
<i>Littorina neritooides</i>	80	Spawned as eggs	Lebour, 1937
<i>Nodilittorina cincta</i>	80	Spawned as eggs	Pilkington, 1971
<i>Nodilittorina unifasciata antipoda</i>	80	Spawned as eggs	Pilkington, 1971
<i>Echinella trochiformis</i>	90	Spawned as eggs	Lebour, 1945
<i>Littorinopsis scabra</i>	100	Eggs retained in mantle cavity, spawned as veligers	Struhsaker, 1966
<i>Littorinopsis melanostoma</i>	120 - 140	Spawned as eggs	Berry and Chew, 1973
<i>Littorina littorea</i>	130 - 170	Spawned as eggs	Linke, 1933; Fretter and Graham, 1962
<i>Bembicium nanum</i>	200 - 210	Veligers hatch from benthic egg mass	Anderson, 1961
<i>Bembicium auratum</i>	230 - 265	Veligers hatch from benthic egg mass	Anderson, 1962
Non-pelagic development to crawling juvenile:			
<i>Littorina saxatilis</i>	485	Ovoviviparous	Fretter and Graham, 1962
<i>Laevilittorina caliginosa</i>	500 \pm 60 SD	In egg mass	This paper
<i>Macquariella hamiltoni</i>	540 \pm 120 SD	In egg mass	This paper
<i>Littorina littoralis</i> (= <i>obtusata</i>)	600	In egg mass	Fretter and Graham, 1962
<i>Laevilittorina coriacea</i>	600	In egg mass	Picken, 1979
<i>Laevilacunaria bennetti</i>	700 - 800	In egg mass	Picken, 1979
<i>Laevilacunaria antarctica</i>	800 - 1,000	In egg mass	Picken, 1979
<i>Pellilittorina pellita</i>	1,500 - 1,750	In egg mass	Picken, 1979
<i>Pellilittorina setosa</i>	1,500 - 1,750	In egg mass	Picken, 1979

□ Nomenclature changes for some species are according to Rosewater (1970) and Bandel and Kadolsky (1982).

* Egg diameter across egg membrane.

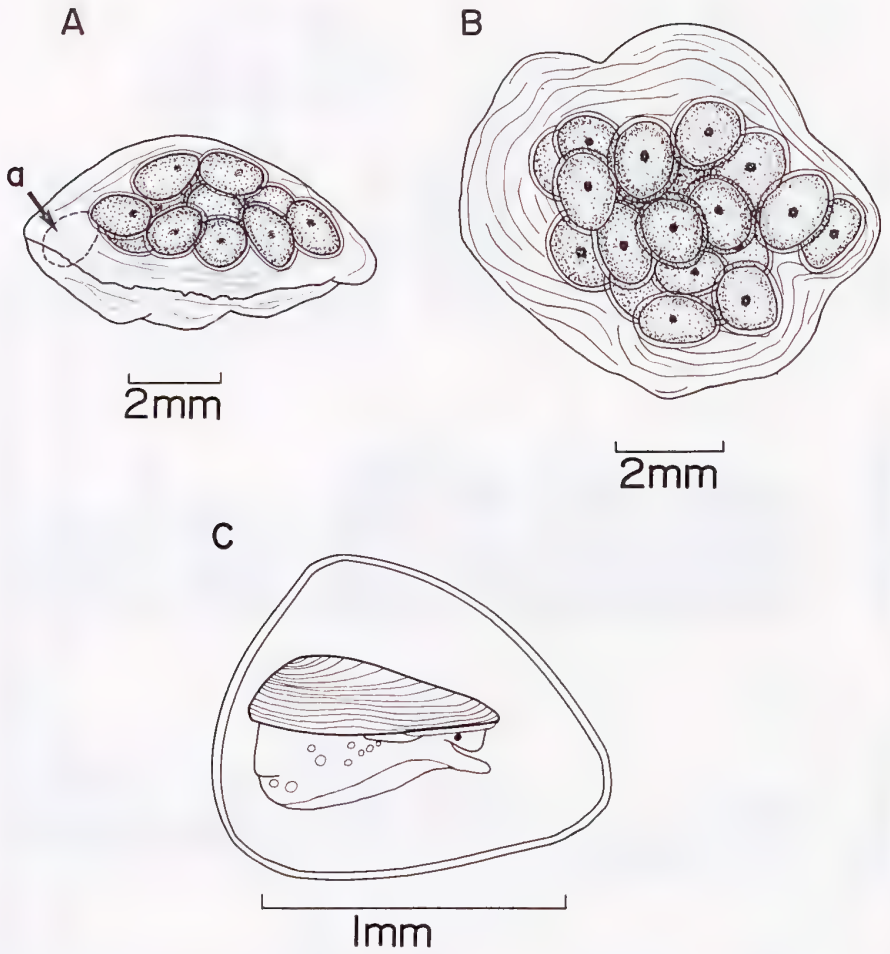


Fig. 1. *Kerguelenella lateralis* : A — lateral view of egg mass (a = empty egg compartment); B — dorsal view of egg mass; C — late stage embryo, prior to hatching.

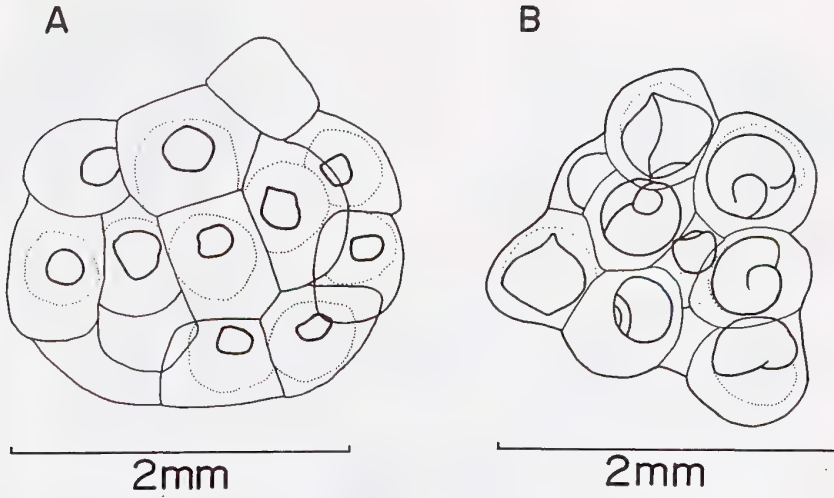


Fig. 2. *Laevitorina caliginosa* : dorsal views of egg masses with early stage embryos (A) and late stage embryos (B).

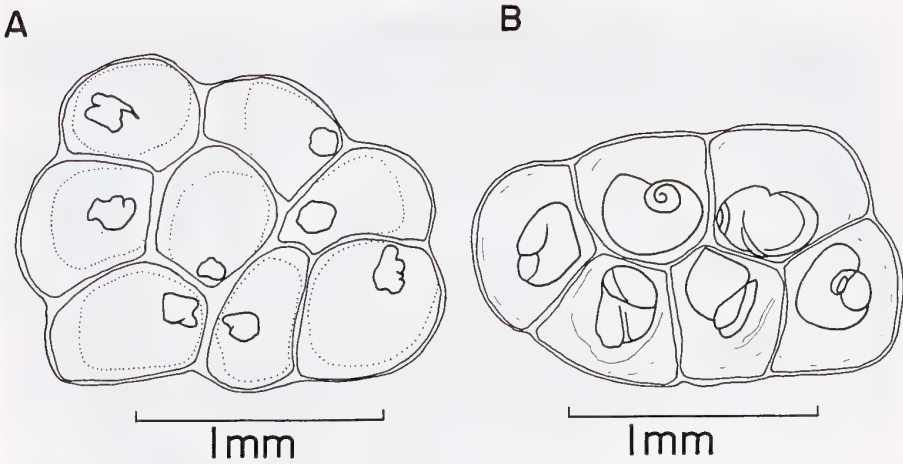


Fig. 3. *Macquariella hamiltoni* : dorsal views of egg masses with early stage embryos (A) and late stage embryos (B).

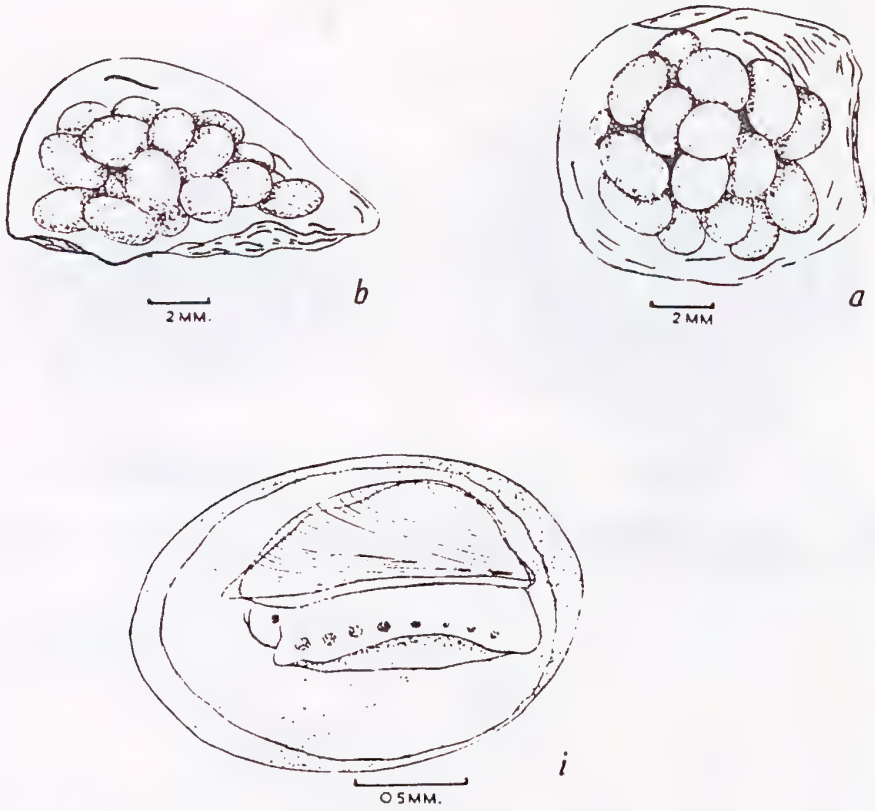


Fig. 4. Egg masses and late stage embryo of *Kerguelenella stewartiana*: b — lateral view of egg mass; a — dorsal view of egg mass; i — fully developed larva ready to emerge. From Knox (1955).